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Studies on the ecological distribution of the genus *Tegula* at Bodega Bay, California

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College of the Pacific
Stockton, Calif.

STUDIES ON THE ECOLOGICAL DISTRIBUTION OF THE
GENUS *TEGULA* AT BODEGA BAY, CALIFORNIA

A Thesis
Presented to
the Faculty of the Department of Zoology
College of the Pacific

In Partial Fulfillment
of the Requirements for the Degree
Master of Arts

by
Allen Emmert Breed
June 1950

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INTRODUCTION

Prosobranch molluscs of the genus Tegula are among the most abundant gastropods on the coast of California, ranging extensively from Sitka, Alaska to Lower California. Because of their abundance and large size they constitute excellent experimental material along the Pacific Coast as does the genus Busycon of the Atlantic Coast. To date, however, there is no ecological study of the genus Tegula on the Pacific Coast that could be used as a guide to any future studies. Most of the work that has been done on Tegula has been taxonomic in nature and the validity of some of the species has been questioned. A concise study on the marine molluscs and brachiopods of Monterey Bay, California, and vicinity has recently been published by the California Academy of Sciences (Smith and MacKenzie, 1948). This work, however, is primarily taxonomic in nature and it is believed that a complete and concise ecological study of the genus Tegula would reveal much valuable information as to the behavior, structure and activities of other gastropod genera.

The lack of study on this genus may be due, in part, to the fact that it is thought by many to be of no economic importance. Tegula funebris and Tegula brunnea do have economic importance. Many ecological surveys are done by the government because the organisms involved are

important as food or destroyers of food. Italians on the Monterey Peninsula collect and boil them in oil, thus making a delicacy of alleged epicurean delight. The whole snail is boiled in oil and the muscular foot is eaten with the help of a pin. Furthermore, depletion of Tegula in any area, such as the Monterey Peninsula, could in some way destroy the food chain or upset the balance of nature, thereby causing a problem that could be of great economic importance.

This paper is primarily a study of the factors contribution to the distribution of Tegula funebris and Tegula brunnea in the vicinity of Bodega Bay, California. The two species seldom appear extensively together in the same zone. Tegula brunnea is found on the exposed outer coast of Tomales Point, but not in the immediate zone of Tegula funebris. Tegula funebris is found at some points north of Dillon Beach, but it is rarely in the presence of abundant Tegula brunnea. The writer hopes that his efforts may lay a basis for more ecological studies of this genera on the Pacific Coast.

The writer is indebted to Dr. Alden E. Noble, Professor of zoology and Director of the Pacific Marine Station, for guidance, inspiration and encouragement. Thanks are also due to Mr. Ferdinand Ruth, Professor of

zoology, Monterey Peninsula College for collaboration in the search for pertinent literature, and to Dr. John R. Arnold, Professor of zoology, College of the Pacific, who gave generous photographic aid in the preparation of plates. Thanks are also extended to Dr. Joel W. Hedgpeth who is responsible for the writer's interest in marine ecology.

Description of Species of Tegula.

Although only two species of Tegula have ever been reported in the area of the mouth of Tomales Bay, there is a possibility of six species on the Pacific Coast.

The following is a review of the six species and the possible subspecies.

Tegula brunnea (Philippi).

Between the tides and on the surface of rocks. Abundant offshore in kelp beds. Extreme low tides uncover large and more thriving specimens. T. brunnea fluctuosa (Dall) has been described by workers but is of doubtful taxonomic value. The forms are weakly differentiated.

Tegula funebris (A. Adams).

Abundant on rocks between the tides and higher up

than T. brunnea. The subspecies T. funebris (Carpenter) is of doubtful taxonomic value. Its validity has been questioned by authorities.

Tegula gallina (Forbes)---Monterey (Dall).

The National Museum possesses some specimens collected by Dall, but as yet there has been no recent authentic record of this species in the Monterey area. It is primarily a southern species. This record is in need of confirmation. It has a solid shell, mostly black in color, but finely mottled with a lighter shade, like the feathers of a speckled hen.

Tegula ligulata (Menke).

This species is also in need of confirmation. This species is called the Banded Topshell. It has a strong solid shell, whose rusty brown whorls are banded with raised spiral lines. These lines are broken or beaded and sometimes are dotted with black, giving the shell a very characteristic appearance. The umbilicus is large and distinct, the aperture circular, and marked below with rounded knobs.

Tegula montereyi (Kiener).

Scarce. Found at low tide on kelp. Offshore kelp

beds must be searched in a boat. Known to occur with T. brunnea but further down the frond. The shell is called the Monterey Topshell, and is strictly conical, with its whorls almost perfectly flat. The base likewise is flat and circular, with almost obsolete spiral lines. The columella does not spread around the umbilicus, which is funnelshaped, is white within, and has its edges defined by an angle. The color is light brown or olive, and the height of the shell, which approximately equals the diameter, is an inch or more. This shell is rare and was formerly thought to be identical with Tegula pfeifferi (Philippi), which is confined to Japanese waters.

Tegula pulligo (Martyn).

With the above, but scarcer. Young specimens are lavender and brown. At Monterey Bay they have been dredged down to 15 fathoms on shale beds. It is possible that the true T. pulligo is a northern race with a rounded basal periphery, (syn. T. pulligo taylori Oldroyd), and the Monterey specimens may be T. marcida (Gould). The Monterey shells have a sharply keeled periphery. This species is known as the Dusky Topshell, and very closely resembles the above species. Its whorls, which number seven, are flattened, and its base is slightly convex, not lined, obliquely streaked, concave

and white around the deep and wide umbilicus, which gradually expands and is partly covered by a white callus, and has no spiral ridge within. The color is dull purplish or brown, often orange when worn. The height of a large specimen is an inch and a half, the breadth about an inch and a quarter. The specimens from Monterey are dark red and distorted.

Portions of these descriptions are from the work of Keep (1935, revised) and Smith and MacKenzie (1948).

Descriptive Details of the Genera of Bodega Bay.

Subgenus Chlorostoma Swainson, 1840.

Tegula funebris (A. Adams), 1854.

This species is similar to T. gallina in form and character of the aperture (plate I). It is lusterless, purple or black, the apex usually eroded, orange colored; the teeth of the columella are white; and there is never a yellowish streak at the base. The whorls are spirally lirate above. The suture is margined below by an impressed line, and by elevated, foliaceous incremental lamellae. This last feature may be usually detected, although sometimes but very slightly developed. Alt., 35; diam., 32; alt., 25; diam., 26 mm. (Tryon and Pilsbry, Manual of Conchology).



Tegula brunnea

Tegula funebris

PLATE I

TEGULA FUNEBRALIS AND TEGULA BRUNNEA

Tegula brunnea (Philippi), 1848.

Shell imperforate, conical, solid, russet-yellow, brown, orange-colored, or deep crimson; spire conic; sutures deeply impressed; whorls about seven, convex, smooth, obliquely lightly striate, the last sometimes obsoletely undulated or plicate below the suture; base depressed, deeply concave in the center; aperture very oblique; columella one-or two-toothed near the base; umbilical callus white; place of the umbilicus deeply excavated. Alt., 32; diam., 36; alt., 38; diam., 35 mm. (Tryon and Pilsbry, Manual of Conchology).

AREA OF OBSERVATION

This work was done at the Pacific Marine Station, Dillon Beach, California, 38° 15' 2" latitude and 122° 57' 58" longitude (plate II). Dillon Beach is ideally located for marine biological studies. It is on the Marin County coast of central California, fifty miles north of San Francisco Bay and thirty miles south of the mouth of the Russian River. Dillon Beach faces the open sea at the mouth of the eighteen mile long Tomales Bay, and is near the southern extremity of the mouth of Bodega Bay. Within a radius of one mile are located exposed and sheltered rocky shores, exposed and sheltered sand beaches, mud flats, shores of boulders and pebbles, salt and brackish marshes, fresh water ponds and streams, sand dunes and fossil beds.

According to Light (1941) the eastern shore of Tomales Bay is a part of the bed of the ancient pleistocene Merced Sea. Along most of this shore the Merced deposits have been eroded, exposing the older Franciscan remains of possible Jurassic origin. In the northeastern portion and along the shores of Bodega Bay, the Merced deposits remain. The conspicuous rocky exposures east of Dillon Beach, known as Elephant Rock, formed part of the shores of the Merced Sea, and the rocks studied in relation to this paper at Perch Rock and

Second Sled Road are evidently from the Merced or from Franciscan deposits. The three portions of this general area which were selected for study are described later in this paper.

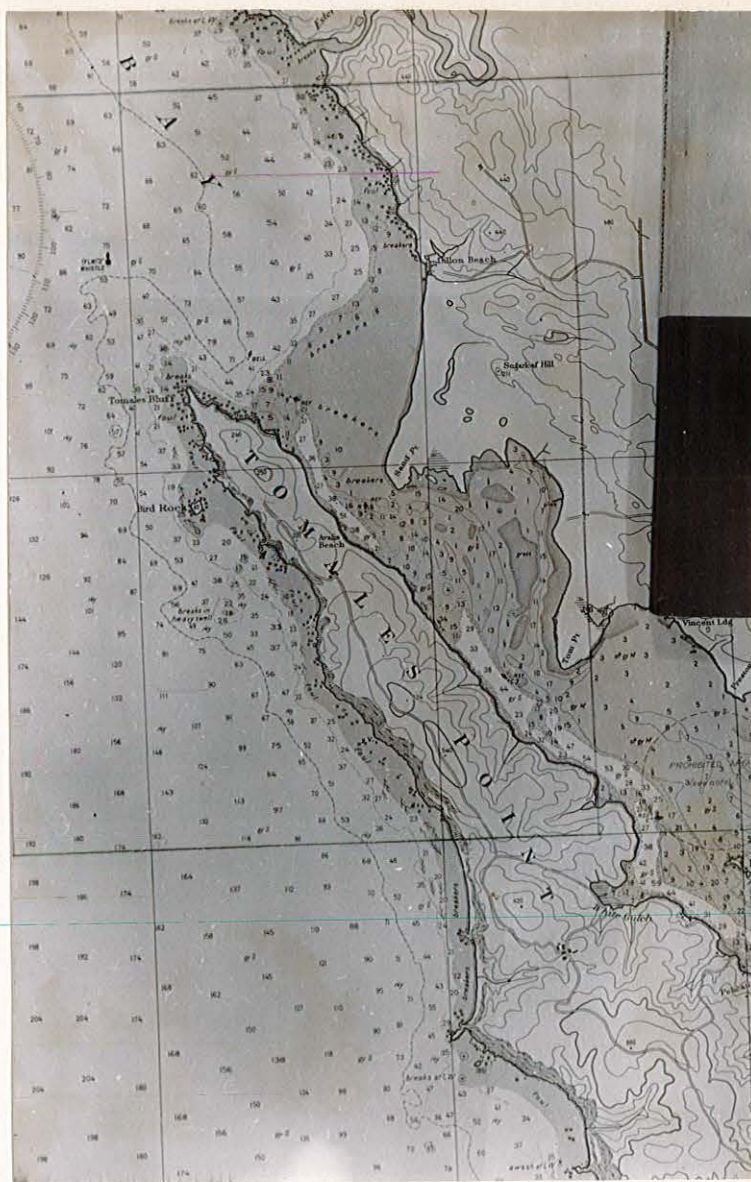


PLATE II

THE AREA OF STUDY

METHODS AND EQUIPMENT

Field equipment consisted of one collecting bucket, one small spirit level, a trench knife, one small stiff-backed notebook, a fountain pen with black waterproof ink, a twelve inch ruler, 150 feet of clothes line cord, a centigrade thermometer, a small hand lens, one six foot pole, a Coast and Geodetic Survey Map of Bodega Bay and Tomales Bay.

The spirit level, six foot pole and the clothes line cord were used to measure the seaward extension of tide levels at the various rocky points studied. The seaward extensions are not available on maps of the area. The measurements of seaward extension were obtained by sighting on the pole with the aid of the level and checking with the clothes line cord. The knife was used for cutting kelp in the search for specimens of Tegula brunnea. The five-cell flashlight was used for night observations at stations I and II (plate III).

Quart bottles were used for transportation of sea water and also for the transportation of specimens from the field stations to the laboratory. The ruler was used for measurement of tide pool depths. When tide pools were too deep to be efficiently measured with a ruler, the clothes line cord was used. The centigrade thermometer

measured temperatures of the air and water.

Laboratory equipment consisted chiefly of one medium sized aquarium, some large culture bowls, some syracuse watch glasses, a dissection kit, dissecting and compound microscopes. The aquarium was used for more prolonged and detailed observations on the behavior of Tegula, chiefly its locomotion and feeding habits. The internal viscera were removed from the shell by boiling the animal for ten or fifteen minutes in water. This method also hardened the body tissues for dissection purposes.

In preparing the radula for study the head of the snail was removed and placed in a solution of potassium hydroxide to which some alizerine red stain was added. This was allowed to stand for a week. This technique completely separated the radula from the animal. The radula was then removed from the potassium hydroxide and alizerine red and transferred to distilled water for three hours. After dehydrating in a graded series of alcohol, the radula was cleared in xylene and mounted in clarite.

Periodic visits were made in the field from the summer of 1949 to January 1950, at the areas described in order to study factors and conditions that affected the genera in their localities. Specially picked tide pools were observed frequently during the fall months of 1949



PLATE III
THE FIELD EQUIPMENT

and activities of the individuals in the pools were recorded. Air, water and sand temperatures were also recorded. Periodic visits at night to the stations were valuable in evaluating nocturnal activities. The floral and faunal contents of the tide pool and its environs were carefully studied in order to determine contributions to the success of Tegula at any given area. Specimens were brought back to the laboratory for dissection and observation and many were subsequently returned to their respective localities. Each species was studied in relation to: (1) horizontal and vertical distribution, (2) floral and faunal associations, (3) relative sizes expressed in length, width, and height, (4) shell surface, (5) variations in radulae, (6) migrations, (7) behavior, (8) food and feeding, (9) oxygen needs, and (10) enemies.

ECOLOGICAL OBSERVATIONS

Station I Perch Rock

Station I is located at an area known as Perch Rock (plate IV). This area is directly adjacent to the sandy beach and is the dividing line between a sandy and a rocky protected outer coast. Consequently, we find that this area is subjected to much shifting sand between the rocks. The writer has observed rocks to be visible above the sand one day and covered with sand another day. Limitation in the growth of plant life is an important factor contributing to the restriction and distribution of the animal life at Perch Rock. Shifting sands control algal growths as well as otherwise affecting the condition of the tide pools from day to day. The tidal area is backed by a 50 foot cliff of clay and granite rock. There is a definite and wide zonation.

Tide pool A.

This tide pool is at the 6' level in the region of the uppermost beach from the highest reach of spray and stormy waves to just below the mean of all high tides (Ricketts and Calvin 1948). It is located in reference to tidal zonation as the upper part of zone II and adjacent to zone I. The depth of this pool is no more than 8" at any point. The pool is four feet long and two



PLATE IV
PERCH ROCK AREA

feet wide.

This pool is at a surprisingly high level for T. funebris. Specimens at other places that have been observed were usually found at the lower level on rocky bottoms in zone II or at a medium position in zone II.

The position of the pool in relation to the surrounding strata, is at the foot of the fifty foot granite cliff which overhangs the tide pool. The tide pool faces west and is shaded even in the late afternoon because of large boulders that shelter the tide pool from the west. Tide pool A contains many crevices under the cliff and the individuals in this pool are distributed in clusters along the crevices. Individuals in this tide pool are medium sized.

The faunal association includes Ligyda occidentalis, found just above tide pool A on the vertical surface of the granite cliff. With this Isopod is Littorina planaxis, Balanus glandula in areas directly above tide pool A and surrounding the pool. Acmaea digitalis is moderately abundant as well as Hemigrapsus nudus which is found in the crevices above and in the pool. Pagurus is conspicuously absent.

The most important floral associate seems to be the

lichen Arthopyrenia litoralis (Leight). This lichen is the only floral growth in the tide pool. It forms a brown incrustation along the smooth rock bottom of the tide pool. The coralline alga Calliarthon cheilosporioides (Manza) is present in tide pool A.

Tide pool B.

Another tide pool about one foot higher than tide pool A is merely a basin gouged out of the rock cliff at the 7' level. Surprisingly, a few adults of T. funebris were in this pool. The only means of getting to this pool by the individual is across the sand and up the side of the cliff for about three feet. Hemigrapsus nudus is abundant here. No alga is present here except the lichen Arthopyrenia litoralis. Pagurus samuelis is not apparent in the tide pool.

Tide pool C.

This habitat is at approximately the 5' level and well into zone II. The pool is about twenty five feet from tide pool A, but differs in many respects from the latter. It is subjected to much shifting sand and is at a much lower level than tide pool A. Tide pool C measures no more than one foot in depth and is approximately four feet wide and four feet long. This pool is open to the

elements from all sides, but large boulders afford shade in the late afternoon. The bottom of this pool is comprised of smooth granite rock with a few crevices. T. funebris is not as abundant in this pool but is more active than the individuals in tide pool A. Visits to this pool were very limited because shifting sand finally covered all of the smooth rock surface, providing no place for T. funebris to adhere.

Common faunal associates include Littorina scutulata which is common around the tide pool on the surface of the boulders, Balanus glandula which is also common around the tide pool and on the surface of the boulders, Thais emarginata which is abundant on surrounding rocks above the water, Acmaea scabra and Acmaea pelta are common, Acmaea limatula is the dominant limpet. The lined shore crab, Pachygrapsus crassipis is conspicuous.

Within the floral association is the lichen Arthopyrenia litoralis incrusting the floor of the tide pool.

Station II Second Sled Road
North of Perch Rock

All zones are well represented in this location and each zone is occupied by several groups of animal species. Rock is more abundant here than at Perch Rock and is of a hard granite type which prevents the occupancy of rock



PLATE V
A SANDY TIDE POOL

borers (plate VI). Sand does not shift because of the distribution of boulders. This results in a great abundance of algae which is the main distinguishing characteristic between this area and the previously described one. Rocks contain small crevices inhabited by small crabs, overhanging rock ledges contain a hydroid-bryozoa-caprellid association. There are more tide pools here than at Perch Rock and less sand to damage them (plate V). The whole area is covered with a hard granite type rock in which water has been caught during the outgoing tide, forming many thriving tide pools.

Tide pool D.

This tide pool is approximately at the same tidal level as tide pool C. The faunal and floral individuals are not confronted with the problem of shifting sand. Tide pool D is well into zone II, but on close examination of the area it is obvious that most of the T. funebris are at a slightly higher level than are the Tegula of tide pool C. Sand is not completely absent from this area, but not in sufficient quantity to be any problem to faunal distribution. Many algae surround tide pool D, but the bottom of the pool is free from any visible macroscopic algae.

The pool measures 15' deep, 6' long and 3½' wide.



PLATE VI
SECOND SLED ROAD

Tegula funebris is more abundant than at tide pools A, B and C, but not as active in the daytime as it is in the latter pools.

Tide pool D is subjected to the elements from all sides, but much visible algae cover the surface of most of the rocks affording protection for roving and sessile fauna.

Some of the Tegula are at the edge of the tide pool hiding in clumps of the alga Prionitis lanceolata (Harvey), but still on the surface of the rocks. There are no more Tegula in the Prionitis lanceolata than in center of the pool.

Faunal associates include Bunodectis xanthogrammatica, Thais emarginata abundant on the surrounding rocks above the water wedged between B. xanthogrammatica, Balanus glandula is common around the tide pool on the surface of the rocks, Littorina scutulata is common around the tide pool and on the surface of the boulders, Acmaea scabra and Acmaea pelta are extremely common, but Acmaea limatula is the dominant limpet. Pagurus samuelis and Hemigrapsus nudus are present, but at a higher level.

Floral associations include the lichen Arthro-

pyrenia litoralis which seems to be more abundant here than at tide pools A, B or C. The lichen incrusts the floor of the tide pool. Prionitis lanceolata, Ulva lactuca and Calliarthron cheilosporioides are present.

Station III East side of Tomales Point

This station is situated on the east side of Tomales Point at the entrance to Tomales Bay (plate VII). The shore line is extremely narrow and zones I and II appear to be combined into one zone. The shore is backed by dirt and granite rock cliffs. Some parts of the beach are composed of granite sand and pebbles, but the main part of this station is composed of smooth, flat-topped porphyritic granite rock. There are not many tide pools in the immediate area of observation, but algae are moderately abundant. There is little surf action at this station because the reef that jets out in an easterly direction from Tomales Point more or less deflects the waves to the main part of Dillon Beach and to stations I and II. Station III is a dividing line between an outer protected coast and a sheltered bay. Consequently, this station is adequately protected from intense wave shock, but is not as thoroughly protected as are the shores of Tomales Bay. Station III is washed by the ingoing and outgoing tidal currents of Tomales Bay.



PLATE VII
THE EAST SIDE OF TOMALES POINT

Tegula funebris is the dominant species in this area. The individuals are clustered together in the crevices of the flat-topped granite rocks in great numbers. This clustering habit is not evident at stations I and II to the effect that it is here, partly because stations I and II are moister areas, abounding in many nutritive tide pools, while station III has no tide pools. In order to alleviate this situation the individuals must retain the moisture in their immediate area by clumping together in crevices and similar places that afford the best opportunity to retain the moisture as the tide goes out. No movement of Tegula was evident in this area during the day as contrasted with stations I and II, but visits to the area in the early evening showed some slight movement.

Arthopyrenia is present in this area as well as Prionitis, but one of the main contributions to the abundance of the Tegula funebris in this area is the reef which protects the snails from heavy wave action. Specimens at this station had the sutures well margined by an impressed line and by elevated, foliaceous incremental lamellae. According to the original description by A. Adams (Oldroyd), 1927 this last feature is present in all specimens, but the writer was unable to detect it in snails subjected to heavy wave action or to the pre-

vailing winds. The incremental lamellae showed slight development in some specimens at both stations I and II on the west side of Tomales Point, but, for the most part, the lamellae were eroded away, especially in older individuals.

Littorina scutulata is abundant in the moist crevices inhabited by Tegula funebris. Littorina planaxis does not appear in this immediate area because of zonal restrictions, although it does appear at adjacent portions of the shore line. Balanus glandula is quite common here on the rocky surfaces, but not as abundant as at stations I and II. Thais emarginata is abundant on the surrounding rocks especially in the crevices inhabited by Tegula funebris and extends in distribution to the zone three level. Acmaea scabra, Acmaea pelta, and Acmaea limatula are present in abundance in the area.

Arthopyrenia litoralis is present here on the more smooth rock surfaces, but not as abundant as it is in the tide pools proper of station I and II. Prionitis lanceolata appears in some of the crevices inhabited by Tegula funebris, but this genus of alga as well as the lichen mentioned above cannot be regarded as common in this area. Many algae are not present here, not because of the shifting sand, as is the case in the other stations, but

because of the dessicating exposure to the sun during most of the day.

Station IV West side of Tomales
Point, Protected

This station is situated on the west side of Tomales Point and faces the open sea. The shore line is extremely narrow and backed by a cliff of rock and sand (plate VIII). Bird Island faces the station. The island is connected to the land by a one thousand yard long reef. The reef is partially uncovered at low tide. It lies at right angles to the north east and therefore affords station IV more shelter than is obtained at other points on the west side of Tomales Point. The same geological formations as were found at station III are also found here, but some are as high as eight feet above sea level. Many protected habitats are found on the side away from westerly exposure. This sheltered condition here contributes to great numbers of Tegula funebris from the five foot to seven foot level (plate IX). The specimens are clustered within protected crevices in order to retain the moisture that gathers in these rocky ledges. Because of this sheltered condition of high rocks and protective reef, Tegula funebris is more abundant here than at stations I and II. The rock at station IV is not covered by much of the alga

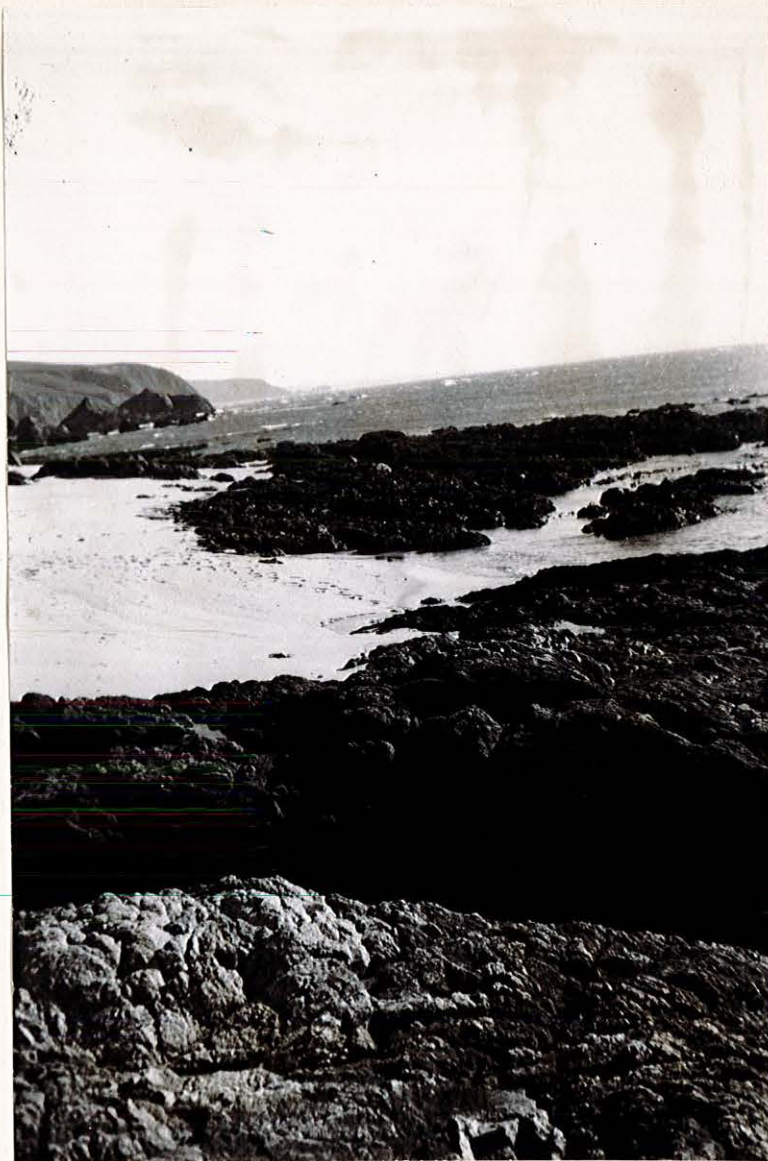


PLATE VIII

THE WEST SIDE OF TOMALES POINT



PLATE IX
A TEGULA FUNEBRALIS NICHE

Prionitis lanceolata. The lichen Arthopyrenia litor-
alis is present. Incremental lamellae are not as evi-
dent on the shells here as they are at station III be-
cause the area is not as protected as is station III.
Tegula brunnea is present at station IV of Tomales
Point. The individuals are at the zone III level and
are submerged under about two to four feet of water.
During low tide they are attached to the fronds of the
kelp Dictyneurum californicum (plate X). More individuals
of Tegula brunnea were found on these kelp fronds than
on any other substrate. Most Tegula funebris are found
on a rock stratum where they can move about and scrape
the Arthopyrenia and other lichens and algae from the
rock surface. On the other hand, it is evident that al-
though Tegula brunnea is found on rocks in the presence
of coralline algae, they prefer to move about on kelp
fronds in about four feet of water. Many specimens were
taken from the kelp holdfasts. Specimens were also
found on the fronds of the kelp Pterygophora calif-
ornica (plate XI and XII).

Bunodactis xanthogrammatica is extremely abundant
in this area and often found in clusters. Thais
emarginata is also abundant here and wedged between B.
xanthogrammatica on the surrounding rocks above the
water. Balanus glandula is common around some of the



PLATE X
DICTYNEURUM CALIFORNICUM



PLATE XI
PTERYGOPHORA CALIFORNICA



PLATE XII
PTERYGOPHORA CALIFORNICA

tide pools in the area. Littorina scutulata is common within the tide pools on the surface of rocks and often clustered with Tegula funebris. Acmaea pelta, A. scabra, A. limatula are common limpets in this locality. Pagurus samuelis occupies empty shells of T. brunnea and T. funebris. Hemigrapsus nudus is found at higher levels.

Arthopyrenia litoralis is abundant here on the more smooth rock surfaces where there is an abundance of T. funebris. Prionitis lanceolata is abundant at the higher levels where T. funebris is found. Ulva lactuca seems to be about the most abundant alga in the area, covering the rocks like a carpet at the lower levels. There are not many algae at the higher levels where T. funebris is found. Calliarthon cheilosporioides, the coralline alga, is abundant on the shells of T. brunnea, as well as on the rocks at the lower levels.

Station V West Side of Tomales
Point, Exposed

This station was chosen for study because it is not protected by the reef, and is subjected to the full force of wind and surf. The shore line is narrow and rocky with few sandy beaches. Rock crevices are abundant, but surf action is intense and Tegula funebris is completely

absent. Where the kelp Ptergophora californica and Dictyneurum californicum are present T. brunnea is found. Both species of kelp are present at this station and T. brunnea is abundant on fronds. During high tide the shore is completely covered by water and during low tide there is much surf action. There is much algal growth on the rocks and Ulva lactuca is primarily dominant. Coralline algae is also abundant here.

DISCUSSION

Aquarium behavior.

In addition to studies in the field, behavior of Tegula was observed in an aquarium where tide pool conditions were simulated as closely as possible.

Most of the movements exhibited in the aquarium were evidently concerned with the procurement of microscopic food. Although the path of slime left by the snail is narrow, the odontophore covers a wider path. As the snail moved in a straight line the odontophore moved from side to side in a sweeping manner. In this fashion the snail covers more area of bottom in its search for food than it would if the mouth merely remained in a straight path as does the rest of the foot. Upon contacting a hard object such as a rock or another snail, Tegula lifts the odontophore from the substrate and applies it in an investigational sort of movement to the object. If apparently favorable, the snail again applies the odontophore in a sweeping fashion and moves the foot upon the object. If the snail applies the odontophore to some incrusting bryozoa it is immediately lifted and reapplied to another area. The solidness and texture of an object apparently determines whether the snail will apply the odontophore upon it or not, for when Tegula funebris

contacts seaweed the tendency is to plow through it and not to lift the odontophore from the surface of the substrate. Even small grains of sand that seem large enough to cause some reaction are brushed aside by the odontophore. Upon reaching a spot where there is much food, the snail will remain in one place while the odontophore sweeps the immediate area. There is a rasping movement of the radula as the odontophore moves over the substrate. The radula slips rapidly over the tip of the buccal cartilage in a rasping movement and dorsal mandible closes over the radula to add a biting motion (Scheer, 1948).

An aquarium was cleaned and filled with fresh sea water. An individual of Tegula funebris was placed in the aquarium and allowed to move from one end to the other. Observations of Tegula funebris seem to indicate that the snail follows the slime track of another snail in its locomotion around the aquarium. The presence of a slime track was indicated by shining a flash light upon the bottom of the aquarium so the light would reflect the slime. Another individual was then placed in the aquarium on a path at right angles to the slime streak, and allowed to move toward the path of the other snail. Each time that this precise procedure was repeated, the snail moved on to the slime path of the first snail and fol-

lowed it across the aquarium, usually to a spot where clumping behavior of the two individuals was apparent. Whether or not this phenomenon is alone sufficient to account for keeping the individuals together cannot be definitely stated. Lack of time prevented conclusive evidence as to this phenonoma being evident in Tegula brunnea.

The same principle of waves of muscular contraction is utilized as in the locomotion of some annelids. Attempts have been made to classify various types of locomotion. Motion may be rhythmic, with regular waves or arrhythmic, without definite wave contractions. The waves may be monotaxic, ditaxic, or even tetrataxic, that is there may be one, two, or even four wave systems on the foot at once. Retrograde waves move along the length of the foot of both species in the opposite direction than the path of the foot of the snail. Direct waves move in the same direction as the path of the animal. The two species seem to be ditaxic in rhythm and in a retrograde direction. The movement is initiated at the foot and travels posteriorly in two waves, one on the left side of the foot and one on the other side. In initiating the contractions, the anterior lateral portion of the foot moves forward causing a wave of contraction to travel in a posterior direction down one half of the foot.

Immediately after the contraction begins, the same movement is initiated on the other lateral side of the propodium causing another wave contraction down the other side of the foot in a posterior direction. Consequently, there are two wave contractions traveling in a posterior direction along the foot, one wave on one side of the foot and one wave on the other side of the foot. It is probable that a double contraction of this sort is more efficient in moving over a rocky surface where there are small depressions than would be a single contraction.

Importance of light.

Both Tegula funebris and Tegula brunnea are apparently negatively phototropic. Aquarium observations showed that the individuals placed at random on the bottom of the aquarium moved to the corner of the aquarium where there was the least amount of light. When the aquarium was turned around so that the shady end was nearer the light and the previously light end was in the shade the snails proceeded to the end of the aquarium where there was the least amount of light. When a light was placed at one end of the aquarium and a dark piece of paper covered the other end of the aquarium the individuals moved away from the source of light to the darker end of the aquarium. There also seems to be a tendency to move

into the corners of the aquarium rather than to remain on the flat surface of the aquarium. This is more apparent in T. funebris than in T. brunnea. Also in tide pools there is a tendency for T. funebris to move into crevices and depressions.

Importance of oxygen.

Aquarium observations seem to indicate that T. brunnea has a greater oxygen need than T. funebris. Specimens of the former brought into the laboratory do not remain active for more than an hour or so even when an areator is operating in the aquarium. Two or three areators must be operating in order to provide enough oxygen. T. funebris will live for days in an un-aerated quart bottle. A particularly active specimen has been living for almost three months in a poorly aerated marine aquarium. These observations suggest one of the factors that may be significant in controlling the distribution of the two species. T. funebris is often found where T. brunnea is but many areas contain only T. funebris. The latter case occurs in those areas where the surf is not active enough, even at low tides to provide the appropriate oxygen need to T. brunnea. This is the probable reason why T. brunnea is not present at Perch Rock and Second Sled Road, and why they are

present on the surf swept western side of Tomales Point. The photosynthetic process of kelp probably contributes to the oxygen supply.

Wave shock.

The topography of the coast line in the vicinity of the mouth of Tomales Bay is such that localities exposed to maximum wave shock and localities almost completely sheltered from the surf both occur within a short distance of each other. The importance of wave shock or its absence as a modifying influence on the faunal distribution in the intertidal area, must be discussed as an all important ecological factor (table I). Whether splash, wash, and spray have a modifying influence on the vertical range of the intertidal animals and plant is known only in a general way. Splash and spray, by raising the effective level of tides, both tend to raise the upper limit of certain species with regard to predicted tidal levels. This was demonstrated by Evans (1947). Moore (1935) has shown that the surf also has a lowering effect on the lower distribution limit of Balanus balanoides, but whether similar effects may be distinguished in other species remains to be investigated. It is obvious from periodic observations, that T. funebris is affected at station I and II by wave

TABLE 1
TYPES OF SHORELINE

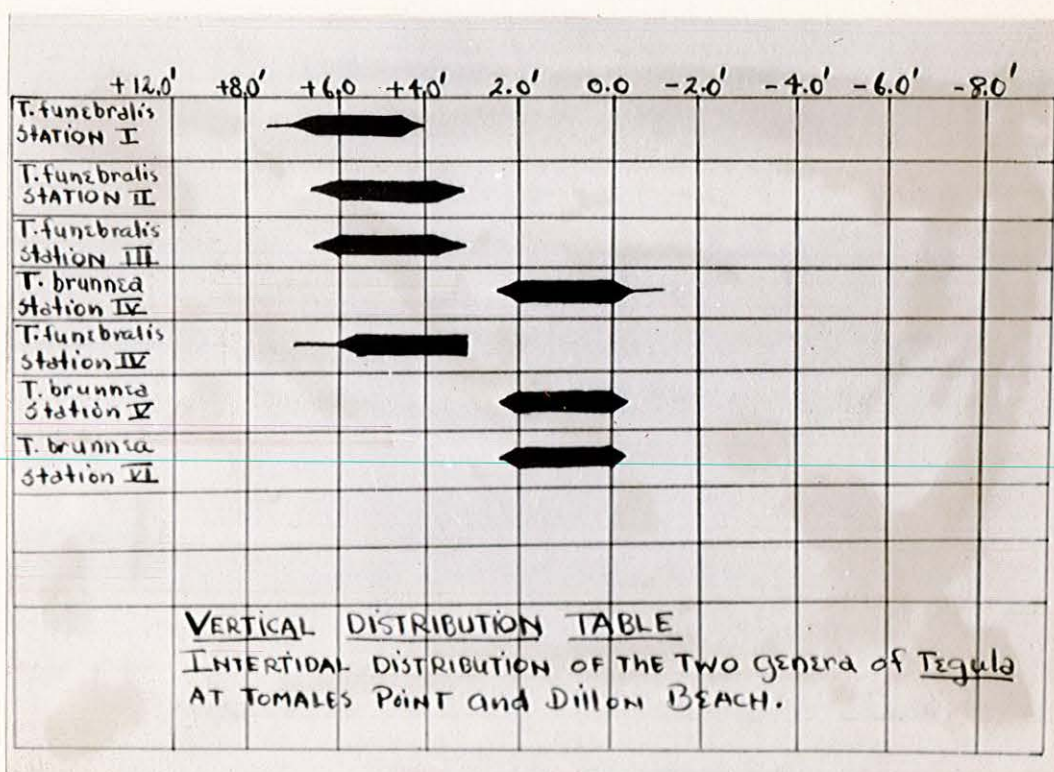
Station	location	exposure
I	Perch Rock	semi-exposed
II	2nd Sled Road	semi-exposed
III	East side Tomales Point.	sheltered
IV	West side Tomales Point.	semi-exposed
V	North of Bird Island	very exposed
VI	Tip of Tomales Point.	very exposed

shock. Although the intensity of the surf, which is moderate at these points, is probably equal, station I seems to have a bit more wave shock than station II. The presence of sand at station I being constantly churned at high tides is possibly the factor that has forced T. funebris to a higher level (plate V). The 7' level is not the usual place to find T. funebris, but only at this level is it free from sand and debris and temporary tide pools. T. funebris must have a permanent tide pool free from sand and debris. At station II T. funebris is found at its predicted level, within the security of permanent tide pools free from sand and debris. Many young specimens of T. funebris were observed at station II but none to speak of were seen either at the lower or upper level tide pools. Most of the individuals at station I were adults. They would not have survived long at station I tide pools under the influence of shifting sand. The fauna and flora in general is scarce at station I compared to station II. Another influence of wave shock upon the gastropod fauna in particular is its power to knock snails from their places of rest and possibly breaking their shells against other rocks. Although Tegula, in general, has much foot pressure, it still seeks the large sheltered tide pools of zone II.

Wave shock in all localities at Tomales Point has

a very definite tendency to raise the zonation of T. funebris. At station III at the east side of Tomales Point T. funebris is found in a relatively sheltered position with few or no tide pools to inhabit. There is actually no wave shock of any importance here because a reef jutting to the north at the tip of Tomales Point diverts the main force of the surf of this area to station I and II. A glance at the vertical distribution table (table II) will show that at station III, T. funebris occupies the same tidal height as at station II. There is no shifting sand at station III to force the species to a higher level such as there is at station I at Perch Rock. Splash, wash and spray seem to have a modifying effect on the upper limits of T. funebris if we take into consideration such stations as I, II and III which vary in their subjection to wave shock but splash and spray raise the effective tide level, wash indirectly forces T. funebris to a higher level by obliterating tide pools with sand. Sand is of great significance in the distribution of T. funebris as can be seen at station I. T. funebris will not tolerate sand although a few have been observed in slightly sandy habitats at station IV on the west side of Tomales Point, south of Bird Island. At this location individuals have become so isolated by the sandy beach that they are un-

TABLE 2
INTERTIDAL DISTRIBUTION



able to move into the higher rocky areas. The sheltered habitat at station III supports one of the largest populations of T. funebris. A hard rocky substrate and a minimum of wave shock, along with the lack of shifting sand, supports a thriving population of T. funebris despite the lack of tide pools. At station III T. funebris is found at the ordinary 5' level.

Station IV on the west side of Tomales Point, south of Bird Island is semi-exposed to wave shock although the dessicating qualities of the wind may be of significance to distribution. As can be seen in the background of plate X, a reef extending one thousand yards from the shore line to Bird Island is the feature that makes this station semi-exposed. Most of the surf is from the northwesterly direction. The reef blocks the oncoming surf forming a more or less semi-sheltered bay between Bird Island and the shore. This sheltering feature favors the development of some isolated populations of T. funebris at about the 5' level. As can be seen by the vertical distribution table (table II) a few individuals are found extending up to the 7' level. Because disservice by dessication by the the wind is such a significant factor to this station, we find T. funebris more abundantly crowded into crevices on the east side of the rocks away from the westerly exposure.

As is the case at station III, station IV has no tide pools. T. funebris are crowded into crevices on a hard rock substrate on the west side of the rocks, completely free from devastating surf action and shifting sand. At a few isolated points lower down on the tidal level, a few T. funebris were observed to inhabit a semi-sandy habitat on hard rocky substrate. There is no possible way for the individuals to get to a higher level because the rocky substrate is completely surrounded by sand.

T. brunnea is extremely abundant at this station. Individuals are found from 0.0' to 2.5' with some extending down to as far as -1.0'. The effect of surf action is not detrimental to T. brunnea as it is to T. funebris. T. brunnea needs the great oxygen supply afforded by a churning surf and green algae. T. brunnea clings to the substrate with more foot pressure and is more adaptable to a constant underwater habitat. At stations V and VI, north of the protective Bird Island, T. brunnea were observed to be just as abundant as individuals at station IV. Foot pressure and underwater adaptability are protective devices against wave shock. It may be possible that wave shock may have a lowering effect on the lower limits of distribution of Tegula brunnea as it does on Balanus balanoides. The existence of kelp in this area

seems more significant in the distribution of T. brunnea than does the effect of wave shock. At no time were any individuals found where there was no kelp Pterygophora californica and Dictyneurum californicum. Although some individuals are frequently found on rock covered with coralline algae, the preferred immediate habitat of T. brunnea is on the fronds of these kelps. The lack of oxygen and the absence of kelp, with the exception of a few individuals of Postelsia sp. is probably the reason for the absence of T. brunnea at stations I, II and III.

Stations V and VI are fully exposed to the open sea. T. funebris does not exist at either of these stations. This is probably due to the great amount of wave shock and lack of protection. T. brunnea is quite abundant here, but no more abundant than at station IV or the southern side of the reef. They are abundant on the kelp fronds of the above mentioned species of marine algae and also are found on the underwater rocky substrates that are covered with incrustations of coralline algae. T. brunnea is able to hold on to the substrate to escape wave shock as well as being protected from wave shock by seeking an underwater habitat.

Food and feeding activities.

All species of Tegula are vegetarian. The food preference of T. funebris at station I and II were studied in field and laboratory in order to determine if any one food was preferred. Late afternoon observations of tide pool activity showed that T. funebris is more active when tide pools are in the shade and the species has a tendency to seek the shady side of the pool. All of the tide pools observed had an incrustation on the underwater surface of the rock. This was identified as the lichen Arthopyrenia litoralis (Leight). Close observation showed that T. funebris moved along the surface of the rock only in the area incrustated with this lichen, carefully avoiding movement on clean rock surface. Individuals removed from the lichen and put on the clean rock surface soon moved into the region of the lichen. Arthopyrenia litoralis was the only floral member present in tide pool A and B, so that it would appear that this lichen is an important part of the diet of T. funebris as well as a means of protective coloration for the snails. The lichen is abundant at station II and seems to have a thicker incrustation than at station I. The possible presence of microscopic algae at the stations must not be overlooked as a possible source of food. Individuals of T. funebris react to the lichen at station II as they

do at station I, but some individuals are found hidden in clusters of *Prionitis lanceolata*. Whether this is a food source or merely a means of protection is yet to be determined. No trace of this alga was found in the alimentary canal.

Rock samples containing the incrustations of the lichen, along with samples of *Ulva lactuca* and *Prionitis lanceolata* were brought into the laboratory for more careful observation of the feeding habits of *T. funebris*. The process by which an animal obtains its food is significant in determining the type of food being eaten. Aquarium observations showed that *T. funebris* moves along the glass side of the aquarium with its mouth always touching the glass. Special movements of the mouth opening show that the individual samples the area and tries to obtain any food particles present. Mouth movements seem to be of the type efficient enough to obtain an incrusting alga. Of fifteen individuals put in the aquarium, ten remained on the rock with the lichen and the remaining five moved off the rock and onto the glass bottom and sides of the aquarium. Individuals of *T. funebris* placed on specimens of *Ulva lactuca* did not eat the alga when put upon it and when it obstructed their path they merely plowed through it without lifting the odontophore from the floor of the aquarium. Since

T. funebris was observed to travel only on the rock surface of the tide pool and only on the floor of the aquarium, we may infer that they eat some small microscopic form of alga such as the lichen Arthopyrenia litoralis. It was also observed not only in the field, but also in the laboratory that T. funebris changed its direction of locomotion upon encountering sand.

Although Tegula funebris at station III did not move along the bottom and sides of the tide pools, it was evident that the lichen was present in this area, incrusting on the rock substrate. The area of station III was free from Prionitis lanceolata.

Individuals of T. funebris at station IV were subjected to the same food conditions as were the individuals at station III. T. brunnea at stations IV, V and VI were probably dieting on the fronds of kelp. Samples of kelp fronds showed lacerations. Close observations of the feeding habits of T. brunnea showed that they moved up and down the kelp fronds constantly scraping off small pieces with their radulae.

The radulae of the two species have the same formulae, but this organ in T. funebris seems to be more delicate than that in T. brunnea. The teeth of the former are smaller and more slender, while those of the

latter are larger, thicker and blunter. According to Cooke (1913) the uncini of Rhipidoglossa are so numerous that they are regarded as indefinite. They are long, narrow and hooked and often cusped at the top. They are long, narrow and hooked in the two genera of Tegula, but they do not appear to have cusps on the top. They are crowded together like the ribs of a fan, those at the extreme edge not being set straight in a formed row, but curving backwards as they become smaller. The average number of laterals in Rhipidoglossa is five. This is the number in both T. brunnea and T. funebris. In both species there is a broad, blade-like center or rachidian tooth. The radula formula of the two species is $\infty.5.1.5.\infty$. The number of teeth in the radula of marine snails varies greatly. When the teeth are very large, they are usually few in number and when they are small they are very numerous. In carnivorous forms, as a rule, the teeth are comparatively few and powerful, while in the phytophagous genera they are many and small as is the case in Tegula. Large hooked and sickle shaped teeth, sometimes furnished with barbs like an arrowhead, and poison glands, are characteristic of genera which feed on flesh. Vegetable eaters, on the contrary, have the teeth rounded and blunter at the apex, or if long and narrow, so slender as to be of comparatively little effect.

Commensals.

There are no empty niches in the intertidal zones because of the keen competition between animals and plants. Not only do animals and plants attach themselves to the firm rock surfaces, but many attach themselves to each other. Many plants and animals attach themselves to marine shells thus affording for themselves a means of transportation and a firm surface for attachment. There were no apparent macroscopic algal growths on the shells of T. funebris. Balanus glandula was found attached to the shell of T. funebris in about one out of ten specimens. Acmaea asmi is abundant on T. funebris. Approximately four out of ten specimens contained Acmaea asmi. No indication of the boring sponge Cliona sp. was apparent. One shell collected had the bryozoa Membranipora membranacea. T. brunnea carried Grepidula adunca on its shell along with the incrusting coralline alga.

Enemies.

The hermit crab, Pagurus samuelis was abundant at station II tide pools, but conspicuously absent at station I tide pools. Pagurus prefers tide pools surrounded by algae and with much sand and debris, and is found at the 5' level and lower, probably extending well into zone III. Many specimens of Pagurus were living in tide pools

inhabited by Tegula and they carried abandoned Tegula shells about with them. Some pagurids carrying Olivella shells were present, but not dominant. Some specimens of Pagurus minus their shells were put into an aquarium in the laboratory in the presence of living Tegula funebris in order to determine whether or not they would attack and clean out the shell. One specimen of Pagurus immediately attacked the living Tegula by bracing himself over the shell and trying to pry it from its position. Other specimens of Pagurus tried this, but no hermit crab was observed to succeed in the effort. Some specimens of T. funebris were put in the aquarium on their backs; Pagurus immediately attacked and tried to pry up the operculum by inserting the claw between the operculum and the shell. This procedure also failed. It is obvious from these experiments with Pagurus that the crab knows how to get at the vital parts of Tegula. It is probably true that they may attack and successfully secure the shell of sick or wounded specimens of Tegula, but that healthy specimens of the snail are too strong and hardy to fall to the attack of these pagurids. The writer did not observe Hemigrapsus nudus and Pachygrapsus crassipis attacking the snail, according to Magalhaes (1948) the chief enemy of Busycon is the sea gull. Her observations showed that the gulls picked up the snails in their

beak and dropped them on the rocks in order to open them. This was not observed in this work. Some tide pool fishes may feed on intertidal snails.

Protection.

Tegula has a thick shell that protects the individuals from dehydration and wave shock. Smooth rock in the absence of sand affords a suitable surface for activities. Apparent ability to migrate from a lower level to a higher protected level is significant in survival of the species. Shifting sand forces T. funebris to area of protective smooth rock surfaces. They are active only during the night and late afternoon or early morning and are more active in the winter and fall than in the summer. The elements may have more of an adverse effect on the species during the winter than during the summer when there are less winds and waves. Protective coloration plays an important part in the distribution and activities of Tegula. The lichen A. litoralis affords a means of protection. T. funebris is more active in tide pools covered with the lichen. This lichen has the same bluish purple tinge as does the shell of T. funebris. When looking into a tide pool from above it is extremely hard to see these individuals at first glance. This lichen could be of aid in protecting the species from attack by

gulls or other sea birds that may feed in tide pools.

T. brunnea usually carries a few species of coralline algae on its back. This pinkish color blended with the brown of the shell blends in well with the environment at Tomales Point because of the extensive growths of coralline algae. As in T. funebris, it is often very difficult to see T. brunnea at first glance for the same reason as stated above. Observation under water is even more difficult.

The submergence of T. brunnea at Tomales Point is significant in protecting the species from wave shock. It has often been observed that in those areas where wave shock is more intense than in others, there are few individuals above the water on the rocks. At station IV where the species is protected from wave devastation by Bird Island Reef there are far more individuals above the water than in such areas north of Bird Island Reef where the surf is heavy. The areas north of the reef show few individuals above the water. In some of these areas algae matting protects individuals from wave shock. T. funebris seeks protection from wave action by moving to the opposite side of the rock. This was observed in station IV.

Tegula funebris taken from moist areas, low on

rocks, and less subjected to isolation, wave shock and the dessicating influence of the wind, possesses thinner and flatter shells than other members of the species in less favorable areas. T. funebris from protected areas had tooth-like imbrications on their shells whereas the individuals from the high exposed situation had a smooth shell.

Migration.

It is obvious from extensive field observations that T. funebris migrates from lower to higher levels; from levels of shifting sand, jagged rock surfaces to areas of no sand and smooth rock surfaces, probably in order to escape shifting sand. This migration that was noticed may be significant in freeing Tegula from Pagurus, for this crab is not found in the higher level tide pools. Migration was not observed at station II to the extent that it was at station I but it was noticed that at station II young Tegula were at a lower level than the adults. No young were above the water, but some adults were above the water in most niches where Prionitis was present.

Relative sizes and proportions.

No appreciable variations in sizes and proportions of T. brunnea were noted at any of the stations. Measure-

ments of T. funebris (tables III, IV and V) showed that there was not much diversity in size at the various stations, although the specimens at stations III and IV had slightly higher shells. These individuals were completely out of the water. Possibly the increased height of the shell permitted increased water content. Individuals at station I and II inhabit tide pools that are more or less permanent and spend most of their time in the water. These individuals had lower spires than those at station III and IV.

Individuals of T. funebris were slightly larger in overall size at station I and II. This is probably because these individuals enjoy a more favorable habitat with an abundance of food and protection. The smallest individuals of T. funebris were found at station IV where the fight for survival against desiccating wind and lack of food must be significant in the survival of the species. The average size of T. funebris at station I is: length, 1.8 cm; width, 1.6 cm; height, 1.0 cm; The average size at station II is: length, 1.8 cm; width, 1.6 cm; height, 1.0 cm; The average size at station III is: length, 2.1 cm; width, 1.9 cm; height, 1.1 cm; The average size of T. brunnea at station IV is: length, 3.1 cm; width, 2.9 cm; height, 2.6 cm.

CONCLUSIONS

Since the oxygen needs of Tegula brunnea are great, the main factors which probably control the distribution of Tegula brunnea are the oxygen content of the water and the presence or absence of the kelps Dictyneurum californicum and Pterygophora californica.

The main factors which control the distribution of Tegula funebris are shifting sand, the lichen Arthopyrenia litoralis on which the species feeds, a moderate amount of shady flat rock surface and an adequate width of intertidal zone.

The two species may be present together on the outer unprotected coast, but in the protected coast areas only Tegula funebris may be present. Tegula funebris is able to adapt itself to varied oxygen contents of the water, whereas Tegula brunnea is not.

TABLE 3
RELATIVE SIZES AND PROPORTIONS

Station II T. funebris 2nd Sled Road centimeters large			Station II T. funebris 2nd Sled Road centimeters medium			Station II T. funebris 2nd Sled Road centimeters small		
L	W	H	L	W	H	L	W	H
2.1	1.9	1.1	1.9	1.7	1.0	1.5	1.3	0.8
1.8	1.6	0.9	1.8	1.6	0.9	1.3	1.2	0.7
2.3	2.1	1.4	1.9	1.8	1.0	1.3	1.2	0.6
2.1	1.9	1.2	1.8	1.6	0.9	1.3	1.2	0.7
2.0	1.8	1.1	1.9	1.7	0.9	1.4	1.3	0.7
2.2	2.0	1.2	1.6	1.5	0.8	1.5	1.3	0.7
2.1	1.9	1.2	1.9	1.7	0.9	1.3	1.2	0.7
2.1	1.8	1.1	1.5	1.5	0.9	1.4	1.3	0.8
2.4	2.2	1.3	1.6	1.4	0.9	1.6	1.5	0.9
2.1	1.8	1.1	1.8	1.6	0.8	1.4	1.3	0.8
2.1	1.8	1.0	2.0	1.8	1.0	1.6	1.4	0.8
2.0	1.7	1.0	1.9	1.6	0.9	1.6	1.4	0.9
2.3	2.1	1.4	1.9	1.7	1.0	1.3	1.2	0.6
1.8	1.6	0.9	1.7	1.6	1.0	1.3	1.2	0.7
2.1	1.8	1.1	1.8	1.6	1.0	1.4	1.3	0.7
2.1	1.8	1.0	1.7	1.0	0.8	1.5	1.3	0.8
2.0	1.7	1.0	1.7	1.6	1.0	1.7	1.4	1.0
2.2	2.0	1.3	1.9	1.7	1.2	1.4	1.2	0.8
2.1	1.9	1.2	1.7	1.5	0.9	1.4	1.2	0.8
2.1	1.9	1.1	1.7	1.6	0.9	1.6	1.4	1.0
2.1	1.9	1.2	2.0	1.8	1.0	1.8	1.6	1.0
2.3	2.1	1.3	1.9	1.7	1.0	1.6	1.4	0.9
2.3	2.1	1.3	1.7	1.0	0.8	1.5	1.4	0.8
2.2	2.0	1.3	1.8	1.6	1.0	1.4	1.3	0.8
2.2	2.0	1.2	1.7	1.6	1.0	1.4	1.2	0.8
2.4	2.3	1.4	1.7	1.5	1.0	1.6	1.4	0.8
2.3	2.1	1.2	1.9	1.8	1.1	1.4	1.3	0.3
2.1	2.2	1.3	1.9	1.7	1.0	1.6	1.5	0.9
2.2	2.0	1.1	1.8	1.6	0.9	1.4	1.3	0.8
1.9	1.7	1.0	1.9	1.7	1.0	1.6	1.5	0.9
2.1	1.9	1.2	1.7	1.5	0.9	1.4	1.3	0.8
2.0	1.8	1.1	2.0	1.8	1.0	1.4	1.3	0.8
2.1	1.8	1.1	1.8	1.6	0.8	1.6	1.5	0.8
2.1	1.9	1.2	2.0	1.8	1.0	1.3	1.2	0.7
2.2	1.9	1.1	1.6	1.5	0.8	1.4	1.3	0.8
2.1	1.9	1.1	2.0	1.8	1.0	1.5	1.3	0.8
1.8	1.6	0.9	1.9	1.6	0.9	1.5	1.3	0.8
2.3	2.1	1.4	1.7	1.7	1.0	1.3	1.2	0.6

TABLE 4
RELATIVE SIZES AND PROPORTIONS

Station IV T. brunnea Tomaes Point Centimeters <small>Large</small>			Station IV T. funebris Tomaes Point Centimeters <small>Medium</small>			Station III T. funebris Tomaes Point Centimeters <small>Small</small>		
L	W	H	L	W	H	L	W	H
3.4	2.9	2.6	2.3	2.1	1.3	2.3	3.3	1.5
3.4	3.0	2.5	2.3	3.0	1.3	2.3	2.1	1.4
3.1	2.9	2.6	2.5	2.3	1.5	2.3	2.2	1.5
2.9	2.8	2.5	1.5	1.3	0.7	2.2	2.0	1.3
3.3	3.1	2.6	1.6	1.3	0.8	2.1	1.9	1.1
3.2	2.9	2.5	1.5	1.3	0.9	2.4	2.0	1.4
2.6	2.5	1.9	1.7	1.6	0.9	2.6	2.4	1.7
2.3	2.1	1.5	1.7	1.5	0.7	2.3	2.0	1.3
2.2	2.0	1.3	2.3	2.1	1.3	2.1	1.9	1.4
1.8	1.7	0.9	2.1	1.9	1.1	2.3	2.1	1.3
1.7	1.6	0.8	2.2	2.0	1.3	2.3	2.0	1.3
3.2	2.9	2.4	2.3	2.2	1.5	2.5	2.3	1.5
3.3	3.1	2.6	2.3	2.1	1.4	1.5	1.3	0.7
3.2	2.9	2.5	2.3	2.2	1.5	1.6	1.4	0.8
3.1	2.9	2.6	1.5	1.3	0.7	1.5	1.3	0.7
2.8	2.7	2.4	2.3	2.1	1.3	1.8	1.6	0.9
3.3	3.1	2.6	2.1	1.9	1.4	1.7	1.5	0.7
3.0	2.9	2.7	1.8	1.6	0.9	2.3	2.1	1.3
3.1	2.8	3.4	2.1	1.9	1.1	2.1	1.9	1.4
3.1	2.8	2.4	2.1	1.9	1.4	2.3	2.0	1.3
2.9	2.8	2.8	2.3	2.1	1.3	2.6	2.4	1.7
3.2	2.9	2.6	2.3	2.0	1.3	2.4	2.0	1.4
3.4	2.9	2.6	2.3	2.0	1.3	2.1	1.9	1.1
3.4	3.0	2.5	2.5	2.3	1.5	2.2	2.0	1.3
3.1	2.9	2.6	1.5	1.3	0.7	2.3	2.2	1.5
2.9	2.8	2.4	1.6	1.4	0.8	2.3	2.1	1.4
3.2	3.1	2.6	1.5	1.3	0.7	2.3	2.2	1.5
3.1	2.9	2.5	1.8	1.6	0.9	1.5	1.3	0.7
2.9	2.8	2.4	1.7	1.5	0.7	2.3	2.1	1.3
3.3	3.1	2.6	2.3	2.1	1.3	2.1	1.9	1.4
3.0	2.8	2.7	2.3	2.2	1.5	1.8	1.6	0.9
3.1	2.8	2.4	2.3	2.1	1.4	2.1	1.9	1.1
3.1	2.8	2.4	2.3	2.1	1.4	1.7	1.5	0.7
2.9	2.8	2.8	2.2	2.0	1.3	1.5	1.3	0.7
3.2	2.9	2.6	2.1	1.9	1.1	2.1	1.9	1.4
3.4	2.9	2.6	2.4	2.0	1.4	1.6	1.4	0.8

TABLE 5
RELATIVE SIZES AND PROPORTIONS

Station I T. funebris Perch Rock Centimeters Large			Station I T. funebris Perch Rock Centimeters Medium			Station I T. funebris Perch Rock Centimeters Small		
L	W	H	L	W	H	L	W	H
2.1	1.8	1.1	1.7	1.6	1.0	1.4	1.3	0.7
2.1	1.8	1.0	1.9	1.7	1.2	1.5	1.3	0.8
2.0	1.1	1.0	1.7	1.5	0.9	1.7	1.4	1.0
2.2	2.0	1.3	1.7	1.6	0.9	1.4	1.2	0.8
2.1	1.9	1.2	2.0	1.8	1.0	1.4	1.2	0.8
2.1	1.9	1.1	1.9	1.7	1.0	1.6	1.4	1.0
2.1	1.9	1.2	1.7	1.0	0.8	1.8	1.6	1.0
2.3	2.1	1.3	1.8	1.6	1.0	1.6	1.4	0.9
2.3	2.1	1.3	1.7	1.6	1.0	1.5	1.4	0.8
2.3	2.0	1.3	1.7	1.5	1.0	1.4	1.3	0.8
2.2	2.0	1.2	1.9	1.8	1.1	1.4	1.2	0.8
2.4	2.3	1.4	1.9	1.7	1.0	1.6	1.4	0.8
2.3	2.1	1.2	1.8	1.6	0.9	1.4	1.3	0.8
2.1	2.2	1.3	1.9	1.7	1.0	1.6	1.5	0.9
2.2	2.0	1.1	1.7	1.5	0.9	1.4	1.3	0.8
1.9	1.7	1.0	2.0	1.8	1.0	1.6	1.5	0.9
2.1	1.9	1.2	1.8	1.6	0.8	1.4	1.3	0.8
2.0	1.8	1.1	2.0	1.8	1.0	1.4	1.3	0.8
2.1	1.8	1.1	1.9	1.6	0.9	1.6	1.5	0.8
2.1	1.9	1.2	1.9	1.7	1.0	1.3	1.2	0.7
2.2	1.9	1.1	1.8	1.6	0.9	1.4	1.3	0.8
2.1	1.9	1.1	1.9	1.8	1.0	1.5	1.3	0.9
1.8	1.3	0.9	1.8	1.6	0.9	1.3	1.2	0.7
2.3	2.1	1.4	1.9	1.7	0.9	1.3	1.2	0.6
2.1	1.9	1.2	1.6	1.5	0.8	1.3	1.2	0.7
2.0	1.8	1.1	1.9	1.7	0.9	1.4	1.3	0.7
2.2	2.0	1.2	1.5	1.5	0.9	1.5	1.3	0.7
2.1	1.9	1.2	1.6	1.4	0.9	1.3	1.2	0.7
2.1	1.8	1.1	1.8	1.6	0.8	1.4	1.3	0.8
2.4	2.2	1.3	2.0	1.8	1.0	1.6	1.5	0.9
2.1	1.8	1.1	1.9	1.6	0.9	1.4	1.3	0.8
2.1	1.8	1.0	1.9	1.7	1.0	1.6	1.4	0.8
2.0	1.7	1.0	1.7	1.6	1.0	1.6	1.4	0.9
2.3	2.1	1.4	1.8	1.6	1.0	1.3	1.2	0.6
1.8	1.6	0.9	1.7	1.0	0.8	1.3	1.2	0.7

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